J. Anat. (1972), **112**, 1, pp. 125–136
With 18 *figures*
Printed in Great Britain

Morphology of the retina of the sea-snake, *Pelamis platurus*

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(*Accepted* 22 *March* 1972)

INTRODUCTION

The venomous sea-snake, *Pelamis platurus*, occupies a unique place among the reptiles. It is the most pelagic of extant reptiles, being born alive at sea and perhaps never going ashore during its lifetime. It is the most wide ranging of the sea-snakes, living in tropical waters from the west coast of South and Central America through the Pacific and Indian Oceans to the east coast of Africa, but is absent from the Atlantic (Moore *et al.* 1965). Sea-snakes belong to the family *Hydrophiidae* and are closely related to snakes of the terrestrial family *Elapidae*, including the cobras, coral snakes, tiger snakes, and kraits, all of which are venomous.

Pelamis has an elongated head, a laterally flattened paddle-shaped tail, and a body covered by very small scales. It feeds on fish, which it catches by a rapid sideward thrust of the head, striking the fish with its short, fixed fangs. The venom, thought to be a neurotoxin, quickly paralyses the prey, which is then swallowed whole. The sideswiping movement of the head indicates that the snake attacks its prey as the latter moves across the lateral visual field, but the snake's attention can be attracted by wiggling an object outside the wall of an aquarium containing the snake, in which case it views the moving object binocularly. When fish are introduced into an aquarium containing a number of sea-snakes, the snakes appear to become aware of their presence, perhaps through the senses of olfaction and taste rather than sight, and begin striking nearby moving objects indiscriminately, often striking each other rather than the fish. Although the snake suffers no deleterious effects when struck by other snakes of the same species, this behaviour, as well as the structure of its retina, suggests that its visual acuity is poor. This handicap may be compensated for by retinal modifications enhancing its ability to perceive motion in the visual field and adjusting for great differences in the intensities of illumination. Its visual cells differ from diurnal elapids which have three types of cones (Walls, 1942), and its retina is very thin but apparently adapted for bright light vision.

MATERIALS AND METHODS

The eyes of eleven sea-snakes, which had been collected alive off the Pacific coast of Mexico by Dr W. A. Dunson, were used in these studies. Eyes of the semi-aquatic mangrove snake *Natrix valida* were also studied by both light and electron microscopy for comparative purposes.

Silver stained sections for light microscopy

Snakes were anaesthetized by being placed for about 20 minutes in an airtight box with a wad of cotton soaked with 1·5 ml of Halothane inhalation anaesthetic. They were then fixed by perfusion with reptilian Ringer's solution followed by Bodian's (1936) fixative introduced into the aorta by cannulation through the ventricle of the heart, with outflow provided by an opening in the right atrium. The descending aorta was either clamped or tied off to direct the perfusate through the carotid arteries into the head.

Following perfusion, the eyes were removed, a slit was made behind and parallel to the corneoscleral junction, and the lens was removed. After fixing for at least 24 hours, the eyes were dehydrated through a graded series of alcohols, embedded in Paraplast, and sectioned at 10 μm. Sections were serially mounted on slides and stained by Bodian's protargol method (1936). Some sections, fixed and embedded as above, were stained by the periodic-acid Schiff (PAS) method for glycogen (McManus & Mowry, 1960), the Azure B method for nucleic acids, both RNA and DNA (Flax & Himes, 1952), or the Feulgen method for DNA (Lillie, 1954).

Golgi–Cox preparations for light microscopy

Following anaesthesia, snakes were fixed by perfusion with reptilian Ringer's followed by 10 % formalin in Ringer's solution. In one case, the snake was perfused with Ringer's solution followed by Golgi–Cox fixative (Cox, 1891). Eyes were removed, opened, and left in Golgi–Cox solution in the dark for a period of six weeks. They were dehydrated, embedded in Parlodion, and sectioned at 40 μm. The free sections were then intensified with ammonium hydroxide, counterstained with cresyl violet, dehydrated, and serially mounted on slides.

Electron microscopy and examination of thick epoxy-embedded specimens

Snakes (both *Pelamis platurus* and *Natrix valida*) were anaesthetized as above by Halothane inhalation. Eyes were removed, opened, and cut up into small pieces in 2 % OsO_4 in 0·1 M phosphate buffer. They were left for one hour in this fixative, then were dehydrated through an ethanol series and embedded in Spurr (1969) resin medium. Thin sections, about 50 nm, were cut with an LKB Ultratome III and mounted on uncoated copper grids. The sections were stained for half an hour each with 0·5 % uranyl acetate and lead citrate (Reynolds, 1963). Sections were examined with an Hitachi HU-11C-1 electron microscope at 50 kV.

Thick sections, about 0·5 μm thick, were stained with toluidine blue (Bencosme *et al.* 1959) for examination by light microscopy. Some were stained by the PAS method for glycogen. Unstained thick sections were also examined by phase microscopy.

RESULTS

In silver-stained sections of the retina of *Pelamis platurus* prepared for light microscopy, the most striking feature immediately discernible in tangential sections is the remarkable development of the horizontal cell processes in the outer plexiform layer (Figs. 3, 5, 9). In Golgi–Cox preparations each of these cells is seen to possess a

number of thick processes (usually four to six) extending like spokes from the large cell body. EM pictures show fibrillar structures present in the cytoplasm of these processes. In addition to the large processes, which extend over a distance of about 550 μm in the outer plexiform layer, there are several smaller, shorter processes in the vicinity of the cell body and a single, smooth process which extends inward through the bipolar cell layer to terminate in the inner plexiform layer (Figs. 9, 10).

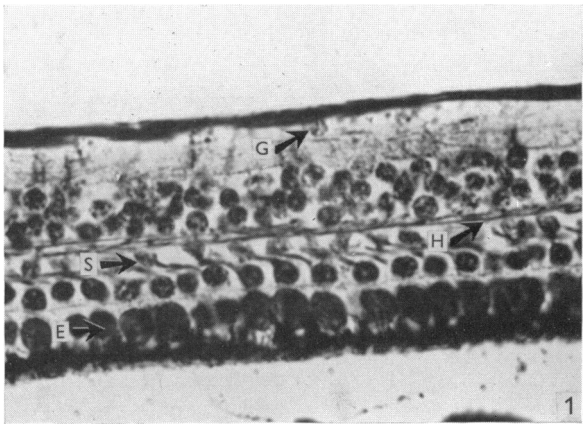
Transverse sections show the retina to be thin and composed of only four or five cell layers; a single layer of photoreceptors, two or three layers which include bipolar, horizontal, and amacrine cells, and a single layer of ganglion cells.

The photoreceptor cells appear to be primarily Type A single cones according to Walls's (1942) classification of snake cones, although EM examination of the outer segments indicates that two cell types may be present. While the tips of some outer segments are pointed (Fig. 16), others appear to be squared off at the tip (Fig. 17). Although no differences were seen in the ellipsoid bodies which would indicate the presence of rods, it is possible that such ellipsoids could have been missed in EM sections if rod-type receptors were present but widely scattered among the large cones. The morphological differences seem very slight indeed and the rod-like outer segments may represent an intermediate condition in the conversion of cones to rods (Type C rod-like cones) similar to that described by Walls (1942) in semi-nocturnal colubrids and elapids. Without the appropriate physiological tests to determine the spectral sensitivity of their pigments, we tentatively suggest that these photoreceptors form an almost pure cone retina. In addition to the short, tapered outer segment, the visual cells possess a large inner segment which contains the ellipsoid body, a short thick myoid, a cell body with a nearly spherical nucleus, and a large synaptic pedicle extending into the outer plexiform layer on a long, thin neck (Fig. 1). Cone doublets of the type found in many snakes, Type B cones of Walls (1942) and Underwood (1970), have not been observed. Oil droplets are absent, as are well-defined paraboloid bodies, but a dense accumulation of PAS positive material is present in the myoid region of the cells.

The ellipsoid body contains mitochondria arranged as in other snake retinas (Yamada, Ishikawa & Hatae, 1966; Underwood, 1970), those toward the periphery being smaller and more numerous and those in the centre being large and filled with inclusion bodies. In osmium-fixed, epon-embedded, 0·5 μm thick sections these inclusion bodies, which are PAS positive and presumably composed of glycogen, are arranged in strands which show some orientation parallel to the long axis of the photoreceptor cell. In electron micrographs, they appear as clusters of granules, and in some cases are symmetrically arranged in pairs localized within compartments between mitochondrial cristae (Fig. 13).

In addition to the PAS positive material in the ellipsoid bodies, dense accumulations of PAS positive substances are localized in the myoid region, in caplike regions of cytoplasm over the vitread ends of the nuclei of both photoreceptor and bipolar cells, and in speckles scattered throughout the outer and inner plexiform layers, probably associated with synaptic endings. Filamentous extensions of the Müller cells distal to the external limitans also show intense PAS staining. Fig. 15 is an EM picture of such filamentous extensions, but is not stained by the PAS method.

Sections stained with Azure B indicate that RNA is present in considerable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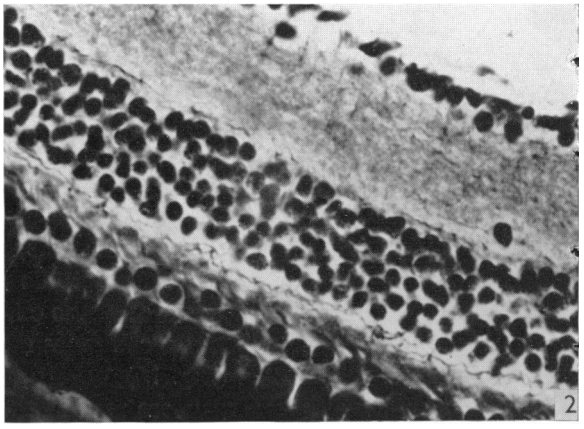
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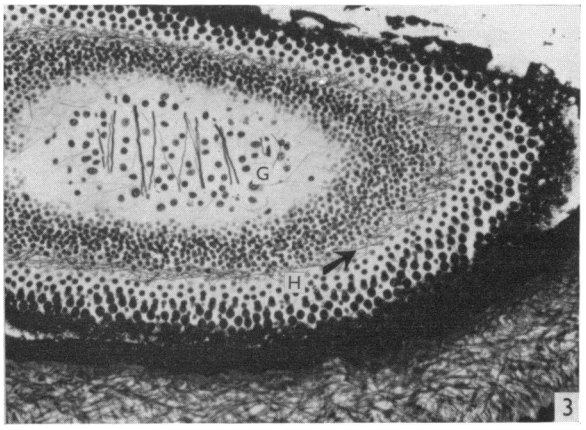
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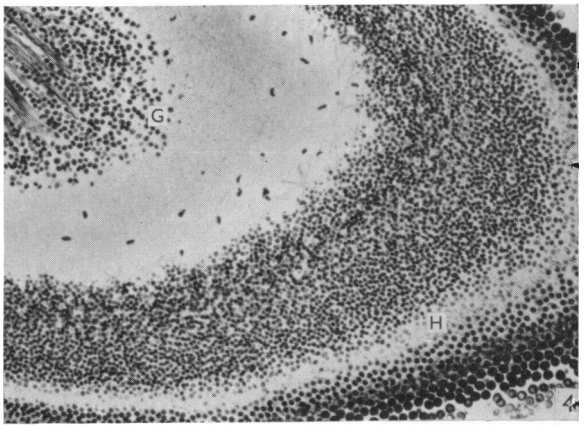
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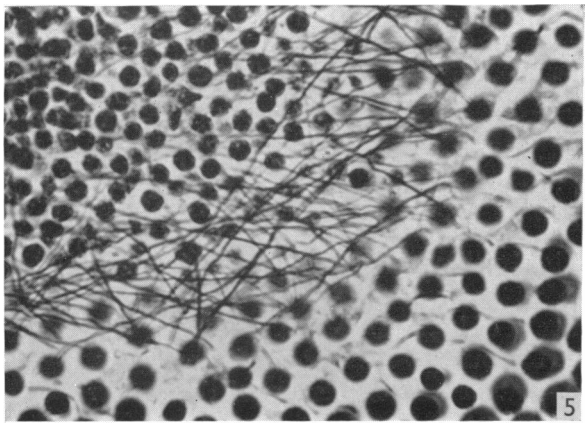
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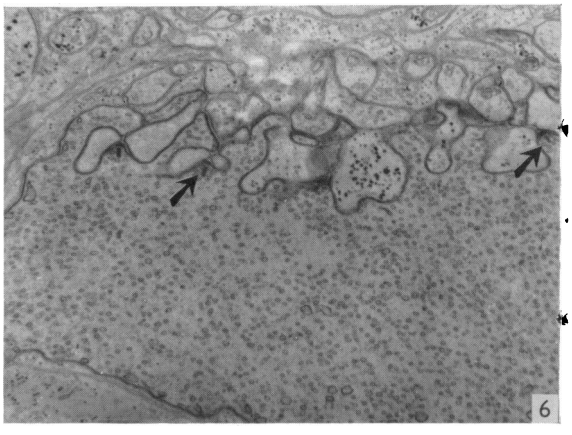
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amounts in the myoid region and in the peripheral cytoplasm of the cell body of the cone, but it ends abruptly at the base of the synaptic pedicle stalk without extending into that part of the cell. Several cones have an RNA-free zone immediately surrounding the nucleus. In Feulgen stained sections, the DNA of the cones and bipolar cells appears to be distributed throughout the nucleus while that of horizontal, amacrine, and ganglion cells appears to be more clumped, perhaps indicating higher template activity in the latter cells.

The synaptic pedicles of the cones are very large, being nearly the size of the cell bodies themselves. There are neurotubule-like structures within the stalk of the pedicle. In addition to being filled with vesicles, each pedicle contains a number of synaptic bars (Figs. 6, 11, 12), and a centrally located membranous structure resembling agranular reticulum. Golgi–Cox preparations indicate that there exists a one-to-one relationship between cone pedicle and bipolar cell (Fig. 10) so that the large number of synaptic contacts made within each pedicle are with a single bipolar cell and one or more horizontal cell processes.

The inner nuclear layer contains the cell bodies of the bipolar cells, horizontal and amacrine cells, and Müller cells, yet this layer is only two, or at most three, cells thick. Each bipolar cell sends most of its dendritic processes in the outer plexiform layer to one cone pedicle but thin branches may contact adjacent pedicles (Figs. 8, 10). Each cell also sends a major process inward to the internal limiting membrane, giving off lateral processes in the inner plexiform layer.

The ganglion cell layer is composed of a single layer of widely scattered cells (Figs. 1, 3). These appear to be of two types, a large cell with extensive diffusely ramifying dendrites having a spread of about 300 μm (Fig. 7), and a smaller cell with a compact dendritic tree extending straight into the inner plexiform layer. The latter type unfortunately stains in clusters by the Golgi–Cox technique, so the processes of a single cell are difficult to trace. At intervals along the dendrites of the larger ganglion cells, bulbous or basket-like expansions are often observed. The axons of the ganglion cells are gathered together in bundles in the optic nerve, which surround aligned rows of glial cells and are enclosed by connective tissue. The bundles interdigitate in the optic chiasma.

Fig. 1. Transverse section through the retina of *Pelamis platurus* showing the large synaptic pedicles (S) and ellipsoid bodies (E) of the photoreceptor cells, the horizontal cell processes (H), the dispersed distribution of ganglion cells (G), and the small number of cell layers. × 485.

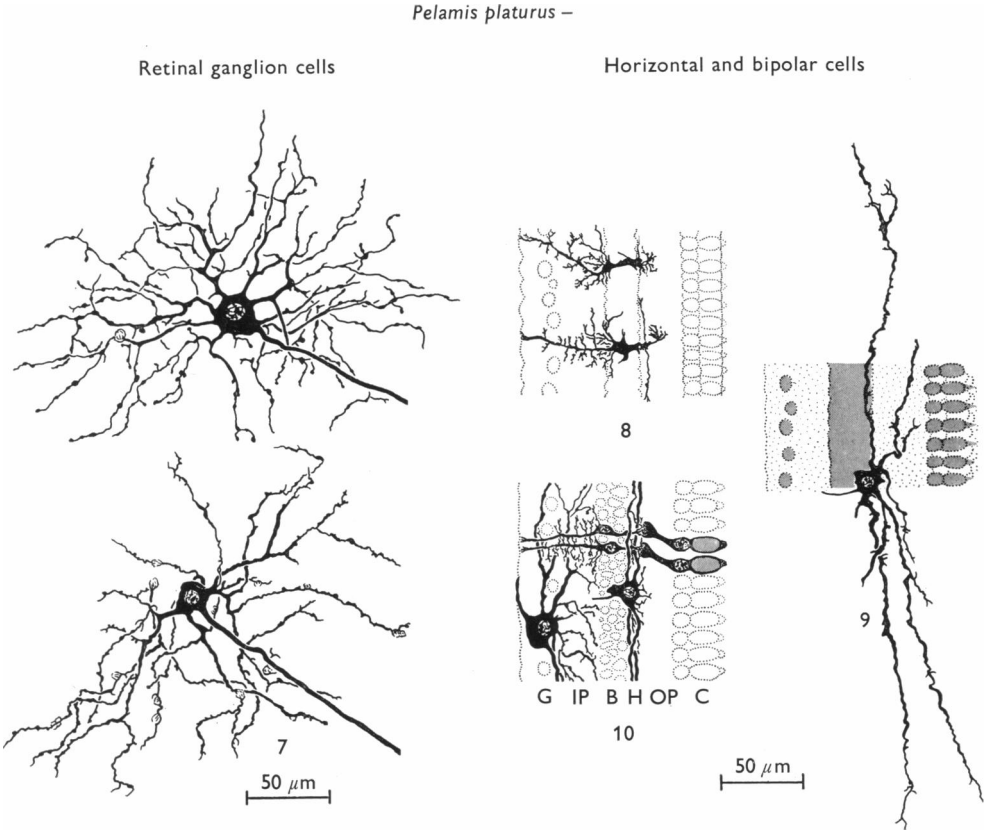
Fig. 2. Transverse section through the retina of *Natrix valida* for comparison with Fig. 1. Note the large number of cells in the inner nuclear layer and the greater thickness of the inner plexiform layer. × 485.

Fig. 3. Tangential section through the retina of *Pelamis* showing the meshwork of horizontal cell processes (H) and the small number of ganglion cells (G) with few but coarse fibres. × 120.

Fig. 4. Tangential section of the *Natrix* retina for comparison with Fig. 3. Note the relative lack of horizontal cell processes (H) and the compact arrangement of the ganglion cells (G) with their numerous fine fibres. × 120.

Fig. 5. An enlarged view of the horizontal cell fibres. Cone nuclei are at lower right, bipolar cell nuclei at upper left. × 485.

Fig. 6. An electron micrograph of a cone pedicle showing four synaptic ribbons, two of which are pointed out by arrows. A conventional synapse may be seen above the left arrow. × 8800.



(Figs. 7–10 represent drawings of retinal cells made from Golgi–Cox preparations. All are drawn at the same magnification.)

Fig. 7. Two ganglion cells viewed from the vitreal surface of the retina.

Fig. 8. Two bipolar cells in a transverse section of the retina. The dendritic processes extending into the outer plexiform layer (OP in drawing below) primarily contact single cone pedicles, but long, thin processes may contact adjacent ones. The major process extending through the thickness of the inner plexiform layer (IP) terminates in a foot-like process at the internal limiting membrane.

Fig. 9. A horizontal cell as seen in a transverse section. Its long, thick, irregular processes extend primarily at the level of the cone pedicles in the outer plexiform layer. It sends a single, smooth process into the inner plexiform layer where it terminates abruptly.

Fig. 10. A drawing showing four major cell types in the sea-snake retina. Amacrine cells are not shown. Layers: (G) ganglion cell, (IP) inner plexiform, (B) bipolar cell, (OP) outer plexiform, (C) cone cell.

DISCUSSION

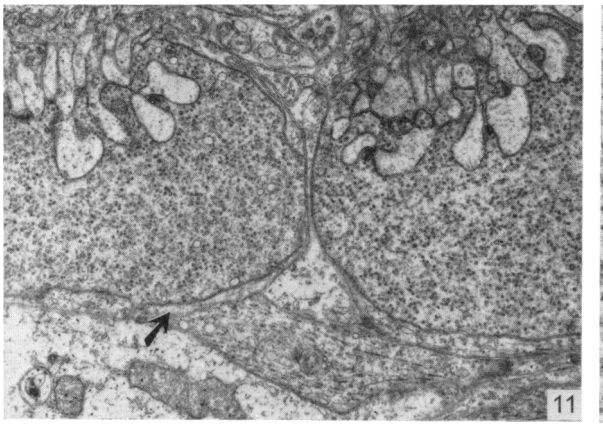
Morphologically, all the photoreceptors in the retina of *Pelamis platurus* appear to be cones, but it is possible that some of them may represent intermediate stages in the transmutation of one cell type to another, such as occurs in the Viperidae (Walls, 1942). In Golgi–Cox preparations, wherever both photoreceptor and bipolar cells stain, each bipolar cell is associated primarily with a single receptor cell. There appears to be little convergence at this level, but the relatively small number of

ganglion cells and the broad extent of their ramifications (Fig. 7) indicates that a considerable amount of convergence and summation occurs between the bipolar and ganglion cell layers. While fine processes of the amacrine cells can be seen in silver stained sections (Fig. 3), they do not stain in the Golgi–Cox preparations. How much these cells, which have been implicated in motion detection in the mudpuppy *Necturus maculosus* by Dowling & Werblin (1969), may be involved in the process of summation in *Pelamis* retina is unclear.

Histochemical stains demonstrate some interesting relationships between localizations of DNA, RNA, and glycogen. Nuclear DNA appears to be uniformly distributed throughout the nuclei of the photoreceptor and bipolar cells, whereas it stains in clumps in the larger nuclei of the horizontal, amacrine, and ganglion cells. This may be related to higher template activity related to maintenance of extensive cell processes. The cytoplasmic RNA in these latter three cell types shows the typical appearance of neuronal Nissl substance. The RNA within the photoreceptor cells is primarily localized in the short myoid region and in the peripheral cytoplasm of the cell body, particularly in the vitread portion, but it does not extend into the neck or synaptic pedicle. The lack of RNA and of mitochondria within the synaptic pedicle indicates that synthesis of the large number of vesicles found there does not occur locally. On the other hand, densely staining PAS positive material is found in the region of the pedicle. The distribution of glycogen in the plexiform layers of this retina indicated by the PAS stain, is similar to that reported by Shimizu & Maeda (1953) who have suggested that the glycogen associated with synapses is located in Müller cells and their processes. Dense PAS positive staining is seen in vitread caps over the nuclei of both photoreceptor and bipolar cells.

The presence of glycogen in the inner segments of the photoreceptors has been reported in a number of species. It is localized in the paraboloid body in amphibians and turtles (Saxen, 1955; Carasso, 1960) and birds (Cohen, 1963), and is present as inclusion bodies in mitochondria of the ellipsoid in snakes (Yamamoto, Ebe & Kobayaski, 1969) and rats (Ishikawa & Pei, 1965). In the snake *Elaphe climacophora*, Yamada *et al.* (1966) reported that inclusion bodies in the ellipsoid were Sudan black B positive granules, suggesting that they contained lipids or phospholipids. While Young (1969) has stated that the ellipsoid body is moderately to heavily stained by lipid stains, this could be due to the presence of lipids within the membranes rather than to the inclusion bodies themselves.

In 0·5 μm thick, epoxy-embedded sections of the retina of *Pelamis platurus*, when stained by the PAS technique, the inclusion bodies in the ellipsoidal mitochondria present a strand-like appearance, densest at the point where the inner and outer segments of the photoreceptor meet, and with the majority of the strands running parallel to the long axis of the cell. This appearance could be due to peripheral localization of the inclusion bodies in the elongated mitochondria, which are also arrayed parallel to the long axis of the receptor. Electron microscopic examination of the receptors indicates that the inclusion bodies are composed of rosettes of individual particles of glycogen, designated alpha particles by Revel (1964), which represent a polymerized storage form of glucose. Young (1969) states that the oxidative pathway of glucose metabolism, a source of energy bearing ATP, is essentially confined to the ellipsoid zone of the photoreceptor. The peculiar symmetrical compartmentalization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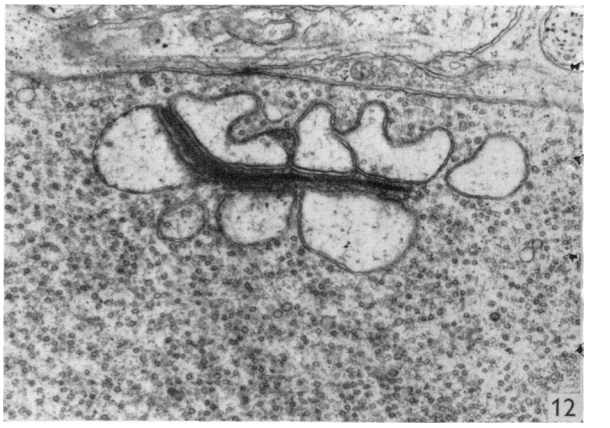
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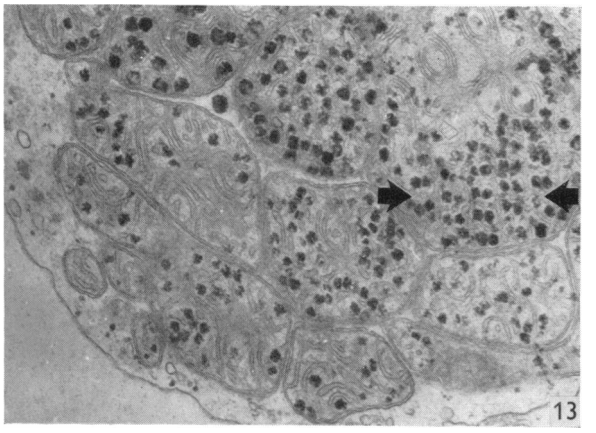
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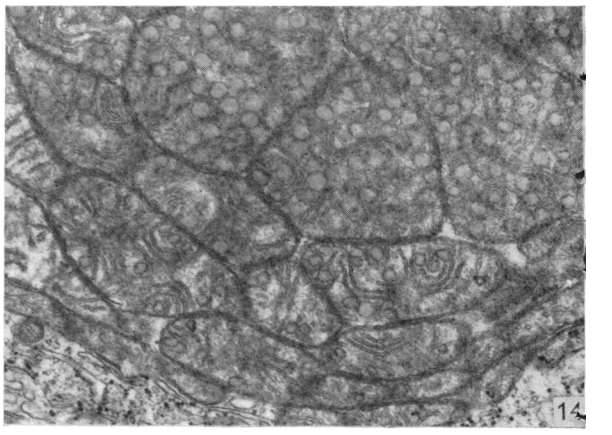
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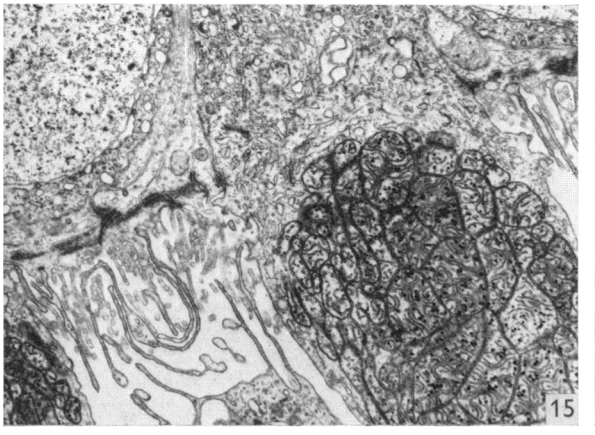
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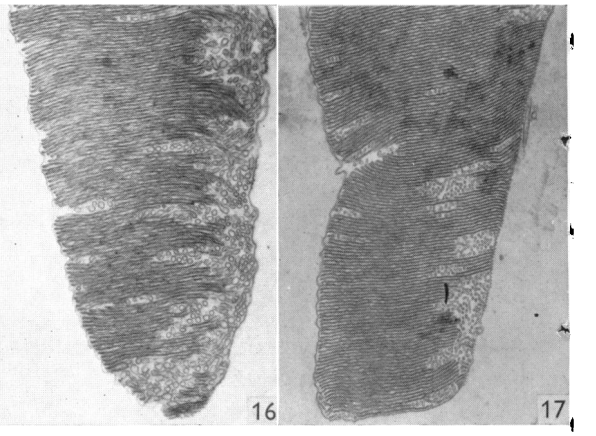
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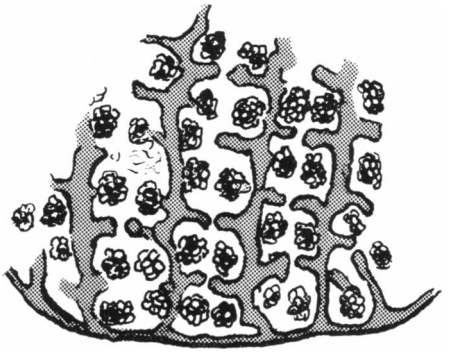

Fig. 18. Drawing of a portion of the central mitochondrion of the ellipsoid shown in Fig. 13 to show the compartmentalized arrangement of glycogen granules between the cristae.

of glycogen particles in the ellipsoidal mitochondria of *Pelamis* would provide maximum surface exposure of the particles to the membranous cristae for rapid mobilization of the energy stores when needed.

A difference in the appearance of the inclusion bodies can be seen when comparing those of *Pelamis platurus* (Fig. 13) with those of *Natrix valida* (Fig. 14). The latter more closely resemble the 'refringent granules' seen in *Vipera berus* (Underwood, 1970) or the 'Sudan black B positive granules' in *Elaphe climacophora* (Yamada *et al.* 1966). Because both the *Pelamis* and *Natrix* retinas were fixed by the same methods, the appearance may represent a basic difference in the state of the inclusion particles rather than a fixation artefact.

In addition to the glycogen granules in the mitochondria of the ellipsoid, metabolic support for the photoreceptors may also be provided by the thin cellular projections of the Müller cells (Fig. 15) which extend beyond the external limiting membrane between the inner segments, as proposed by Pedler & Tilly (1963). These are also heavily stained by the PAS technique.

A major difference between the retina of *Pelamis platurus* and that of *Natrix valida*

Fig. 11. Two synaptic pedicles in the sea-snake retina. Below the one at the left can be seen its neck. Each is supported by a thin cup of cytoplasm, perhaps part of a Müller cell (arrow). × 5550.

Fig. 12. A horizontal section through a synaptic ribbon showing its contacts with several cell processes. × 14850.

Fig. 13. An ellipsoid body of *Pelamis platurus*. Inclusion granules (probably glycogen) are seen in the mitochondrial matrix. Some (between arrows) are symmetrically arranged in pairs within compartments between the mitochondrial cristae. × 37100.

Fig. 14. An ellipsoid body of *Natrix valida*. Although the fixation and staining were the same as for the ellipsoid shown in Fig. 13, the inclusion bodies appear quite different. × 37100.

Fig. 15. Filamentous processes of the Müller cells extending beyond the external limitans. A number of cells apparently contribute to the formation of the limiting membrane between adjacent receptor cells. Part of the ellipsoid is seen at the right. × 5550.

Fig. 16. Scleral tip of a cone showing a large number of tubular elements as well as lamellae. × 14850.

Fig. 17. Squared-off tip of another photoreceptor. This may represent a transitional stage between one cell type and another (see text). × 14850.

is the extraordinary development of the horizontal cells of the former (Figs. 1–4). In the mudpuppy *Necturus maculosus*, Dowling & Werblin (1969) have found that horizontal cell processes invaginate into cone terminals and also make numerous conventional synapses on bipolar cell dendrites. Synaptic ribbons of the type seen in cone pedicles (Figs. 6, 12) are always associated with two or more postsynaptic processes. Werblin & Dowling (1969), studying electrical potentials in the retinal cells of the mudpuppy, found that the horizontal cell response is slower than that of the receptor, but that the horizontal cell summates over a wide area. Its potentials resemble the luminosity type S potentials recorded in fish. The horizontal cell is thought to mediate the receptive-field surround, and to alter the response of the bipolar cell according to the relative amounts of light falling on the receptor cell with which it is in direct contact and on receptors nearby.

What function might the profuse meshwork of horizontal cell fibres serve in the sea-snake retina? Sjöstrand (1969) has suggested that the horizontal cell connections in the eye represent the structural basis for perception of movement and shape. It might well serve such a function in the sea-snake retina, but another possibility is suggested by a consideration of the unique habitat of this snake. While its predatory habits would call for it to view moving objects underwater, it can also distinguish its own enemies at the surface or in the air. How well it can correct for differences in refractive index between water and air is not clear, but an equally important consideration to be taken into account is the great difference between intensities of illumination in the two media. It does not possess some of the protective devices found in turtles, for example, such as eyelids and coloured oil droplets which are supposed to correct for chromatic aberration and to help to reduce the effect of surface glare (Walls, 1942). Prince (1956) suggests that the extremely contractile circular pupil of sea-snakes, which can contract to a pinhole, is both an accommodation mechanism and a glare shield. Under conditions of intense illumination such as might occur at or above the surface of the sea, particularly in the tropics, input from a large number of photoreceptors on to the horizontal cell processes might serve to reduce the stimuli received by the ganglion cells by inhibiting bipolar cell responses near the points where they originate at the cone pedicles. The effect of such diffuse inhibition might resemble the insertion of a neutral density filter into the light path, decreasing light intensity while at the same time maintaining or even enhancing form and pattern discrimination. Efferent fibres, if they are present in the optic nerve of the snake, could also play a similar role.

Under water, where the light intensities are lower, the thinness of the retina, the presence of well-developed horizontal cells, and the summation that occurs between the bipolar and ganglion cells could enhance perception of movement while simultaneously having an adverse effect on visual acuity. Observations on the behaviour of the snakes suggest that their vision is quite adequate but that they cannot or do not discriminate between objects moving within their striking range. Both morphological and behavioural observations support the hypothesis that the retina of the sea-snake *Pelamis platurus* has undergone modifications which may increase the snake's ability to perceive motion both above and beneath the surface of the sea.

SUMMARY

The retina of the pelagic sea-snake, *Pelamis platurus*, is thin, and is composed of few cell layers, with the inner nuclear layer made up of only two or three layers of cells. The photoreceptors appear to be primarily, if not solely, bulky cones having large ellipsoids and very large synaptic pedicles at the inner end of long, thin necks. While several synaptic connexions are made in each pedicle, they are made for the most part with dendrites of a single bipolar cell and horizontal cell processes. The latter are unusually well developed in the sea-snake retina. It is suggested that the horizontal cells play a role not only in motion detection and form vision, but possibly also in reducing the effect of glare under conditions of intense illumination.

The distribution of glycogen in the retina has been studied by both PAS staining and electron microscopy. Inclusion bodies within the central mitochondria of the ellipsoid are composed of glycogen granules. In some cases they are found in a highly ordered symmetrical arrangement with pairs of granules localized within compartments between the mitochondrial cristae. This arrangement would presumably provide maximum exposure of the particles for rapid utilization of energy when required.

The thinness of the retina, the small number of bipolar and ganglion cells, the spacing of the receptor cells, the size of the dendritic spread of the ganglion cells, and the hypertrophy of the horizontal cells indicate that visual acuity may be sacrificed in this retina for adaptations which would enhance perception of motion in the snake's visual field.

This work was supported by grant NS-08662 from the National Institute of Neurologic Diseases and Stroke, U.S. Public Health Service. The authors wish to thank Dr William A. Dunson for supplying the snakes used for this study and Mrs June Arnold for technical assistance.

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